CHAPTER 3

Animal Populations, Biomass and Production

3.1
Soil Invertebrates

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As a part of studies intended to estimate the biological production in the evergreen oak forest of the Minamata IBP area, the density and biomass of soil invertebrates and their seasonal fluctuation were investigated. Although an accurate estimate of secondary production of these animals was difficult from the data obtained in the present study, the gross yearly metabolic rate of total soil fauna was obtainable as an indicator of biological activity of animals using various values of bio-economical terms so far elucidated by numerous authors.

3.1.1 Methods

Sampling A sampling site on a slope between the ridge and one of the permanent plots for primary production (P2) was settled on and serial samples by various methods of collection were taken within a *ca.* 100 m square of the site. Several extraction methods were employed simultaneously for soil mesofauna. For nematodes, soil sample cores of 10 cm^2 in area and top 3 cm in depth were taken and processed by Baermann's funnel. For enchytraeids, soil sample cores of 20 cm^2 and top 3 cm in depth were taken and processed by O'Connor's funnel. Soil samples from various soil depths were taken by almost the same procedure as that described in Kitazawa et al. (1977). For minute soil arthropoda such as collembola and acarina, larger soil samples of 156.25 cm^2 (12.5 cm square) in area and top 10 cm in depth were taken and processed by Tullgren's funnel. The processing times for these method were 24 hours for Baermann's funnel, 3 hours for O'Connor's funnel and 48 hours for Tullgren's funnel. For soil macrofauna, a quadrat (25×25 cm) was placed on the ground surface and soil samples to 7 cm in depth were taken. Animals were sorted out from the soil samples by hand in the laboratory. Usually, some replicate samples were taken for each method. Collections were made in May and October 1968; thereafter, monthly collections were carried out from July, 1970 to October, 1971. However, only part of the samples were used in the present paper for delay of sample processing.

Measurement The body length of individuals of Nematoda and Enchytraeids was measured by an almost identical method with the profile projector-curvimeter method (Tamura, 1974). An electric microbalancer (accuracy is below 0.5 μg) was used for measuring the body weight of tiny animals.

The pattern of spatial distribution for the animals was evaluated by the value of I_δ index (Morisita, 1959) calculated from data of replicate samples by the same method. The 95% fiducial limits for mean values were also determined by the I_δ method (Morisita, 1964; Ono, 1967).

The method for calculation of the gross yearly metabolic rate of total soil fauna is described in a later section.

3.1.2 Numerical density and biomass

3.1.2.1 Baermann's Funnel Method

In the present only the Nematodes are dealt with out of the materials extracted by Baermann's funnel. Figure 3.1–1 shows monthly change in population density for total Nematoda extracted from the soil from the surface to 3 cm in depth. The animals were abundant in spring and in autumn, and less so in summer and in winter. The density of Nematoda fluctuated between 0.2×10^6 m^{-2} in December, 1970 and 2×10^6 m^{-2} in April, 1971.

The seasonal change in vertical distribution of Nematoda is represented in Fig. 3.1–2. There is a slight decreasing trend with the depth of the soil. The animal density in the soil at a given depth may be expressed by the following formula:

$$y=A_0e^{-ax} \tag{1}$$

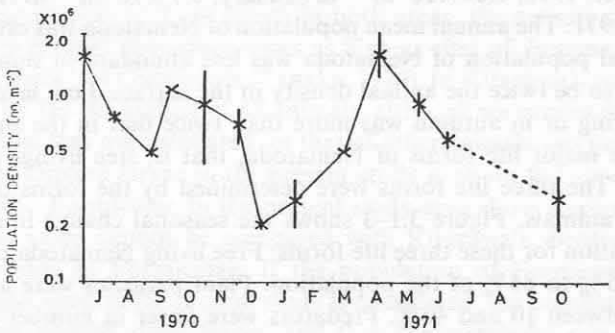

FIG. 3.1–1. Monthly counts of Nematoda population in the soil layer from the surface to 3 cm depth.

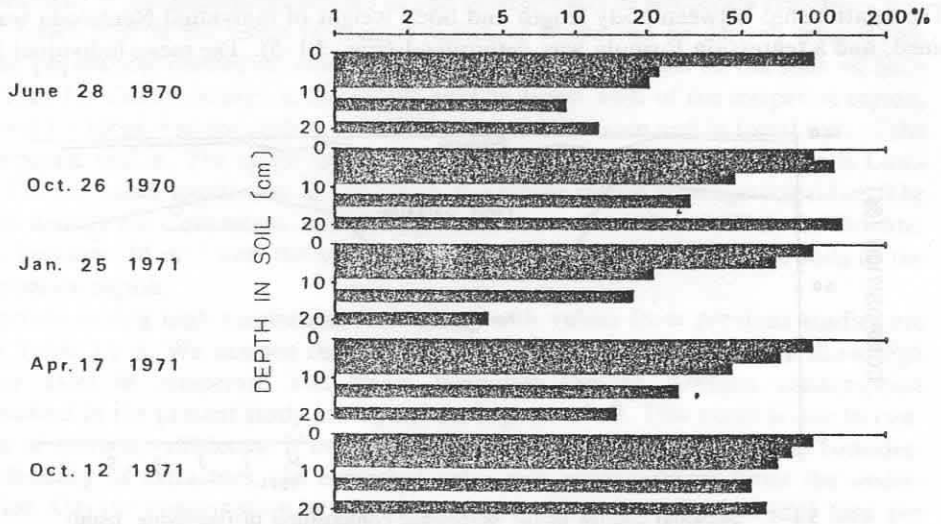

FIG. 3.1–2. Seasonal change in the vertical distribution of Nematoda in soil.

where x is soil depth in cm, a denotes the decreasing rate and A_0 represents the animal density in surface soil. The following values for the decreasing rate, a, were obtained; 0.163 in July, 0.0106 in October 1970, 0.141 in January, 0.0942 in April, and 0.0325 in October, 1971. The decreasing rate is high in summer and in winter and that indicates the animals aggregate in the upper soil. On the other hand, the decreasing rate is low in spring and in autumn, and that suggests slight or no difference in animal densities between upper and lower soils.

The total animal population in the soil from the surface to X cm in depth is estimated by the following equation:

$$Y=\int_0^X \frac{1}{3} y \, dx \qquad (2)$$

where, x and y are the same as in Eq. (1), and the number 3 is a coefficient derived from the depth of a soil core. To calculate the total Nematoda population, the depth X is supposed to be 30 cm. The total population in each month reached 1.49×10^6 m^{-2} in July, 6.29×10^6 m^{-2} in October, 1970, 0.64×10^6 m^{-2} in January, 5.7×10^6 m^{-2} in April, and 2.03×10^6 m^{-2} in October, 1971. The annual mean population of Nematoda was estimated to be 3.23×10^6 m^{-2}. The total population of Nematoda was less abundant in summer and in winter, and was assessed to be twice the animal density in the surface 3 cm layer of soil. The total population in spring or in autumn was more than twice that in the surface soil.

There are three major life forms of Nematoda, that is, free living, plant-parasitic and predatory forms. The three life forms were determined by the forms of the buccal cavity and stylet of the animals. Figure 3.1–3 shows the seasonal change in composition of the Nematoda population for these three life forms. Free living Nematoda constitute the major part occupying 55% to 85% of the population. Plant parasites were abundant in winter, and fluctuated between 10 and 40%. Predators were fewer in number in all seasons, and the population in any month did not reach 5%.

The seasonal change in size composition of the total Nematoda population is illustrated in Fig. 3.1–4. Animals less than 0.5 mm in length were most abundant in any season.

The relationship between body length and body weight of individual Nematoda was examined, and a regression formula was determined (Fig. 3.1–5). The mean individual body

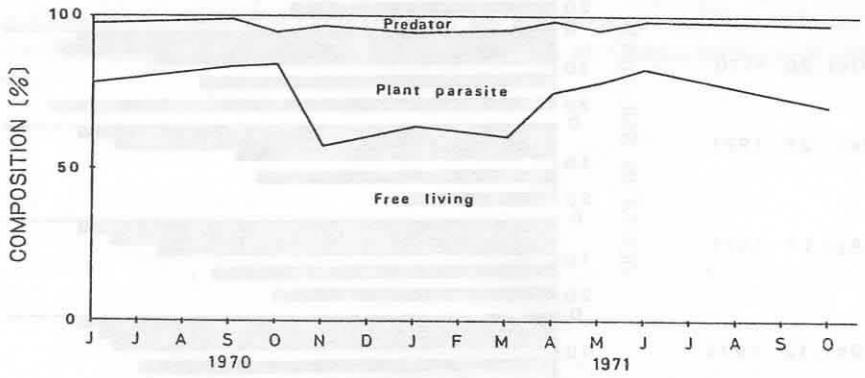

FIG. 3.1–3. Seasonal change in the percentage composition of free-living, plant-parasite and predator populations of Nematoda.

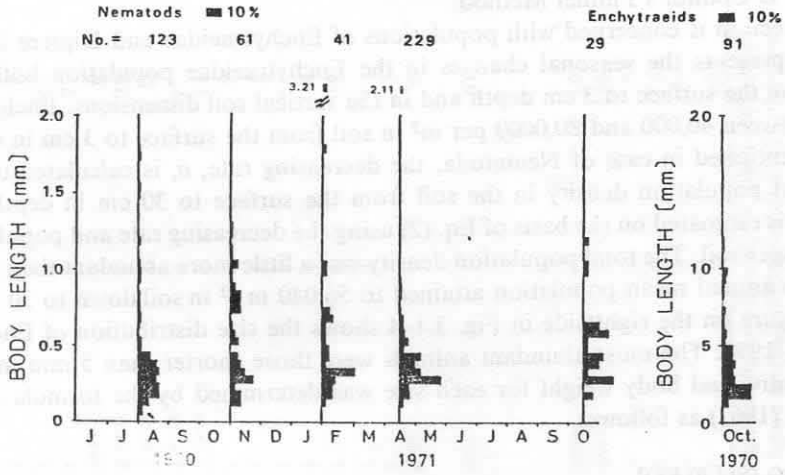

FIG. 3.1–4. Seasonal change in the size composition [%] of Nematoda and the size structure of Enchytraeidae in October.

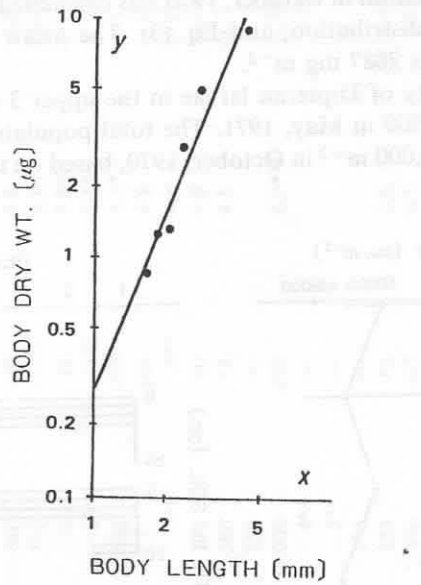

FIG. 3.1–5. Body length–body weight relationship in Nematoda. The straight line corresponds to the regression, $\log y = 2.552 \log x - 0.5634$ ($r^2 = 0.932$).

weight in the population for each month was calculated by the use of data on size composition and the regression coefficients for the body length/body weight relationship.

Yearly mean body weight was estimated at 0.0951 μg dry weight. The biomass of Nematoda in each month was assessed to be 118 mg m^{-2} in July, 604 mg in October, 1970, 125 mg in January, 214 mg in April, and 132 mg in October, 1971. Thus, the estimate of yearly mean biomass was 239 mg m^{-2}.

3.1.2.2 O'Connor's Funnel Method

This section is concerned with populations of Enchytraeidae and Diptera larvae. Figure 3.1–6 represents the seasonal changes in the Enchytraeidae population both in the unit area from the surface to 3 cm depth and in the vertical soil dimensions. Enchytraeids fluctuate between 40,000 and 80,0000 per m^2 in soil from the surface to 3 cm in depth.

As mentioned in case of Nematoda, the decreasing rate, a, is calculated using Eq. (1). The total population density in the soil from the surface to 30 cm in depth for Enchytraeidae is estimated on the basis of Eq. (2) using the decreasing rate and population density in the upper soil. The total population density was a little more abundant than that in upper soil. The annual mean population attained to 56,040 m^{-2} in soil down to 30 cm in depth.

The figure on the right side in Fig. 3.1–4 shows the size distribution of Enchtraeidae in October, 1970. The most abundant animals were those shorter than 5 mm in length.

The individual body weight for each size was determined by the formula presented by Edwards (1967) as follows:

$$W=0.18(L/0.88)^3 \qquad (3)$$

where W denotes the dry body weight in μg for an individual, the value of 0.18 shows the dry body weight/live body weight ratio, and L represents body length in mm. Biomass of the Enchytraeidae population in October, 1970 was calculated on the basis of data on population density and size distribution, and Eq. (3). The mean body weight was 37.9 μg dry weight, and biomass was 2687 mg m^{-2}.

The population density of Dipteran larvae in the upper 3 cm of the soil was 6700 m^{-2} in October, 1970, and 4500 in May, 1971. The total population in the soil up to 30 cm in depth was assessed as 34,000 m^{-2} in October, 1970, based on the decreasing rate (a=0.0517)

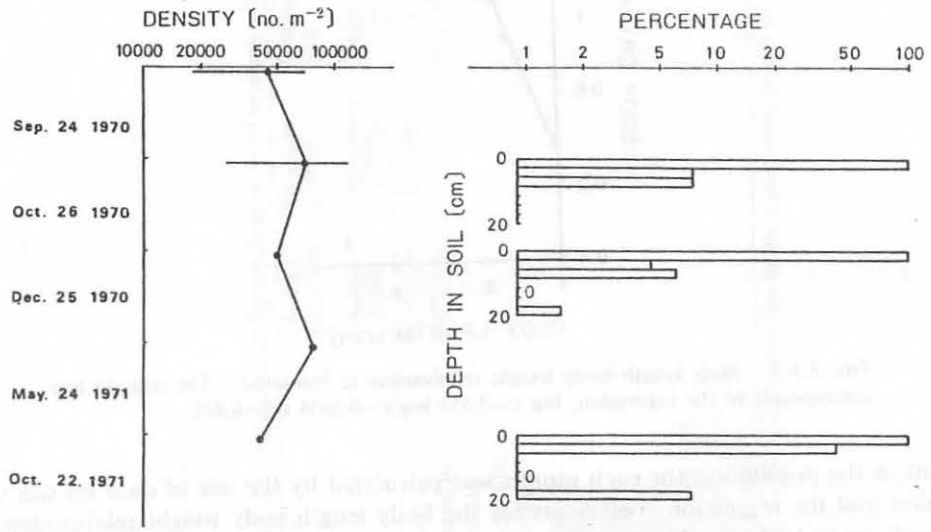

FIG. 3.1–6. Seasonal changes in the population density and vertical distribution of Enchytraeidae. Population densities for three months are given in percentages relative to that in the surface layer (0–3 cm in depth). Horizontal lines indicate 95% fiducial limits for mean value.

TABLE 3.1–1. Collembolan population taken by Tullgren's funnel.

	Number per m²				Mean density per m²	
	1970 Aug.	1970 Oct.	1971 May	1971 Oct.	No.	%
Xenylla ~~humicola~~ brevispina	100				30	0.1
Hypogastrura (s. str.) sp. a		7200	5600		3200	5.5
Odontella (*Clavontella*) *similis*	400	500		1500	600	1.0
Lobella mizunasiana	2100		1500		900	1.6
L. halophila	500				130	0.2
Micranurida cf. *hasai*	300				80	0.1
M. (*Grananurida*) *tuberculata*	100				30	0.1
Pseudachorutes cf. *insularis*	400				100	0.2
P. cf. *longisetis*	2100	1000			780	1.4
Paranura sp. a	1300			500	450	0.8
Neanura (s. str.) *frigida*	100				30	0.1
N. (s. str.) sp. a	500			500	250	0.4
N. (*Vitronura*) *mandarina*	1200			500	430	0.7
Tullbergia (*Mesaphorura*) *Krausbaueri*	800	8700	9700	24600	10950	19.0
Onychiurus (*Protaphorura*) sp. a		2600	2000	1000	1400	2.4
O. (*Paronychiurus*) *flavescens*	4400	9700	7700	6100	6980	12.1
O. (*Pa.*) sp. a	1000		1000		500	0.9
Micrisotoma achromata	600			500	280	0.5
Folsomia octoculata	10500	6100	1500	6100	6050	10.5
F. regularis		500			130	0.2
F. sp. a	400		1000	1000	600	1.0
Folsomina onychiurina	2900	22500	1500	17900	11200	19.4
Isotomiella minor	900		1500	7700	2530	4.4
Isotoma (s. str.) *decorata* cf.	300				80	0.1
Sinella dubiosa	2800			2800	1400	2.4
Homidia sp. a	100		100	500	180	0.3
H. sp. b				300	80	0.1
H. sp. c	300				80	0.1
Entomobrya sp. a	300				80	0.1
Lepidocyrtus lanuginosus cf.	2600	700	600	1100	1250	2.2
L. sp. a	800	100	100	2400	850	1.5
Harlowmillsia oculata	2200			500	680	1.2
Tomocerus (*Monodontocerus*) *mocificatus*	1400				350	0.6
T. (*Tomocerina*) *liliptunus*	2100	100	100	3300	1400	2.4
T. (s. str.) *ocreatus*		100		200	80	0.1
T. (s. str.) *Kinoshitai*	1700			200	480	0.8
T. (s. str.) *violacens*		100	100	100	80	0.1
Neelides folsomi	500			500	250	0.4
Megalothorax incertus cf.	500				130	0.2
Sphaeridia pumilis		500			130	0.2
S. sp. a		500	500		250	0.4
Arrhopalites sp. a	6300		500	2000	2200	3.8
Lipothrix cf. *mirabilis*	100				30	0.1
Ptenothrix sp. a	100				30	0.1
Total	52700	6900	35000	81800	57720	100.0

and population in the surface soil (A_0=6700). Moreover, the mean body weight was 12 μg, and biomass was estimated as 408 mg m^{-2} dry weight.

3.1.2.3 Tullgren's Funnel Method

The soil invertebrates of many taxonomic groups were extracted by Tullgren's funnel. The population density of each species of Collembola is shown for April, for October, 1970, for May, and for October, 1971, in Table 3.1–1. The number of species found in these four months' sampling was 44, and the mean total population was 57,720 m^{-2}. The dominant species were: *Folsomina onychiurina* reaching 11,200 m^{-2} and constituting 19.4% of the total Collembola population, *Tullbergia* (*Mesaphorura*) *Krausbaueri* reaching 10,950 m^{-2} and 19.0%, *Onychiurus* (*Paronychiurus*) *flavescens* 6980 m^{-2} and 12.1%, and *Folsomia octoculata* 6050 m^{-2} and 10.5%.

Table 3.1–2 represents population density and biomass for the taxonomic groups of animals extracted by Tullgren's funnel. The sampling points selected for soil samples in May or in October, 1968, however, were different from the area where samples were taken in 1970 and 1971. Based on monthly mean population, the abundant animals were Collembola at 66,000 m^{-2} in the soil from the surface to 10 cm in depth, Cryptostigmata at 65,800

TABLE 3.1–2. Population density and biomass for soil invertebrates extracted through Tullgren's funnel.

	Number per m^2						Biomass (dry wt mg m^{-2})			
	1968 May	1968 Oct.	1970 Aug.	1970 Oct.	1971 May	1971 Oct.	1970 Aug.	1970 Oct.	1971 May	1971 Oct.
Gastropoda			260		130	130				
Oligochaeta		100	380	830	130	640				
Pseudoscorpione	200	200	320	60	260	700	13	10	13	29
Phalangida	40	100								
Mesostigmata	34500	30000	6270	17660	34060	51970	14	60	129	210
Prostigmata			11260	13060	17410	32260	5	6	4	31
Astigmata			130	4610	2560	16900		2		6
Cryptostigmata			21630	37120	79870	124420	56	79	264	241
Araneae	200	300	320	130	60	450	7	12		13
Isopoda		100	190	60		60	51	9		10
Pauropoda	200	200	320			2180				2
Oniscomorpha	40									
Juliformia	200	100	190	190	700	1660	288	1498	614	608
Geophilomorpha		100				130				755
Lithobiomorpha	40	100	510		60	130	58		8	173
Symphyla	200	500	450	380	190	1220	8	6	8	33
Protura			380	60		960				2
Collembola	25900	35900	56450	59720	41450	106520	152	86	118	146
Diplura				60	60	380				2
Thysanura	40									
Thysanoptera			130	60	190	320				2
Coleoptera	100		640	260	380	130	166	29	60	17
Formicidae	700	200	510	7680	1790	1730	77	813	429	461
Hemiptera larvae	100	900	380	60	830	1540	28		61	36
Lepidoptera larvae	100		580			580	128			390
Diptera larvae	400	100	130	320	700	2110	1	5	26	51
Coleoptera larvae	1100	400	380	60	320	130	64	13	6	4
Insect larvae				60		60				
Total	63900	69000	101810	142440	181140	347310	1116	2628	1740	3222

m^{-2}, Mesostigmata at 27,500 m^{-2} and Prostigmata at 18,500 m^{-2}. Major animals showing high biomass were Juliformia (Diplopoda) at 752 mg m^{-2} and Formicidae at 445 mg m^{-2}. In spite of their low numerical density, some taxonomic groups having large body size show considerably high biomass per area. They are Geophilomorpha (Chilopoda) at 189 mg m^{-2} and Lepidoptera larvae at 130 mg m^{-2}. On the other hand, there were other populations having fairly high biomass, since the number of specimens was large in spite of their small body size. They were Cryptostigmata, 160 mg m^{-2}, Collembola, 126 mg m^{-2}, and Mesostigmata, 103 mg m^{-2}. The figures of density and biomass mentioned above are based on uncorrected data obtained by the funnel extraction method. According to some evidence, however, the efficiency of such extraction methods is not very high. If population density or biomass is corrected by the efficiency coefficient of the extractor, the values mentioned above must be multiplied several times. In the section on gross yearly metabolic rate calculation, correction is made for the mean biomass values of each taxa using the efficiency of extractors in order to estimate more real values of metabolic rates for animal populations.

3.1.2.3 Quadrat Method

Identified species taken by the quadrat method were: in Mesogastropoda, *Cyclotus (Procyclotus) campanulatus*, *Chamalycaeus satsumanus* and *Diplommatima (Sinica) tanegashimae kyushuensis*, in Stylommatophora, *Pseudoneia sieboldii*, *Allopeas kyotoensis*, *Otesiopsis japonica* and *Yamatochlamys (Trochochlamys) crenulata*, in Isopoda, *Porcellionides pruinosus*, *Armadillidium vulgare* and *Ligidium japonica*, in Araneae, *Araneus displicatus*, *Storena hoosi*, *Tmarus piger*, *Anyphaena pugil*, *Anahita fauna* and *Heteropoda forcipata*.

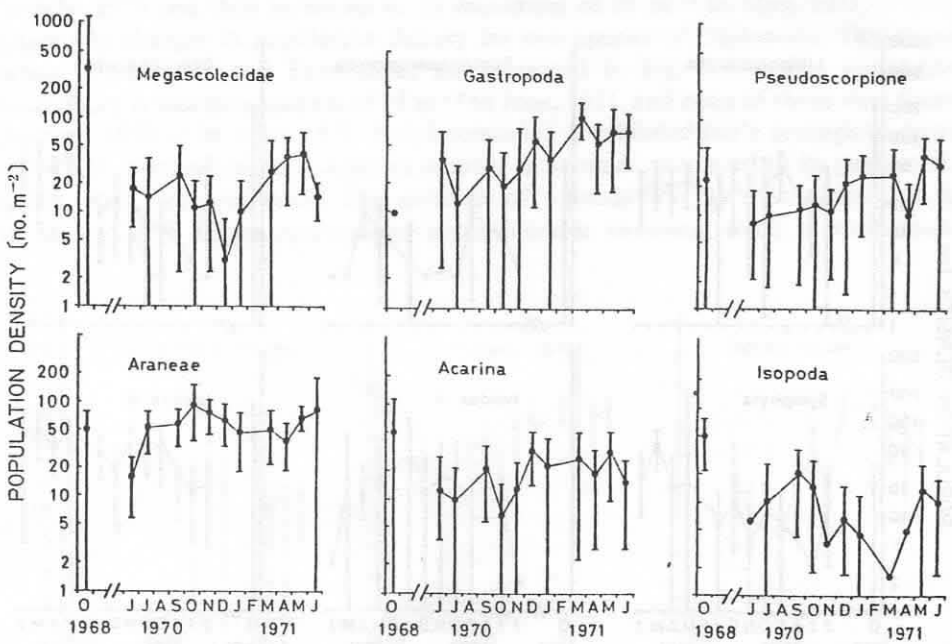

FIG. 3.1-7. Seasonal changes in the population density of Megascolecidae, Pseudoscorpione, Gastropoda, Acarina, Araneae and Isopoda. Vertical lines indicate 95% fiducial limits.

The monthly changes in population density for Megascolecidae, Gastropoda, Pseudoscorpione, Araneae, Acarina and Isopoda are illustrated in Fig. 3.1–7. The pattern of spatial distribution for Megascolecidae was fairly clumped, and the population attained its maximum of 40 m^{-2} in spring and gradually decreased to its minimum of 3 m^{-2} in winter. The spatial pattern of distribution is judged as to whether it is clumped, random or uniform according to the I_δ value, as described in the Methods section. The distributional pattern of Gastropoda was somewhat contagious, and the population density varied between 8 m^{-2} and 40 m^{-2}. Araneae showed random, or more or less contagious distribution, and its density varied between 16 m^{-2} in summer and 94 m^{-2} in autumn. Acarina located by the naked eye indicated a more or less contagious distribution, and its population fluctuated between 6 m^{-2} and 30 m^{-2}. Isopoda exhibited a fairly aggregated distribution, and its population attained 20 m^{-2} in early autumn, thereafter decreased to its minimum of 2 m^{-2} in spring, and then increased again.

The monthly changes in population density for three orders of Chilopoda, Symphyla, and two species of Diplopoda are presented in Fig. 3.1–8. Lithobiomorpha indicated random distribution in spring and fairly clustered distribution in the other seasons, and its population fluctuated between 16 m^{-2} and 45 m^{-2} without clear trends. Scolopendromorpha changed in its population between 3 m^{-2} and 16 m^{-2}. Geophilomorpha showed a slightly contagious distribution, and its population was at its minimum of 5 m^{-2} in the summer of 1970, and thereafter increased to its maximum of 66 m^{-2} in March, 1971. Symphyla showed the same trends in distributional pattern and population change as Geophilomorpha, and its population varied between 3 m^{-2} and 54 m^{-2}. Julidae A exhibited a fairly aggregated distribution, and its population was minimum, 2 m^{-2}, in summer, thereafter increased to its maximum, 42 m^{-2}, in winter and then decreased. Julidae B indicated

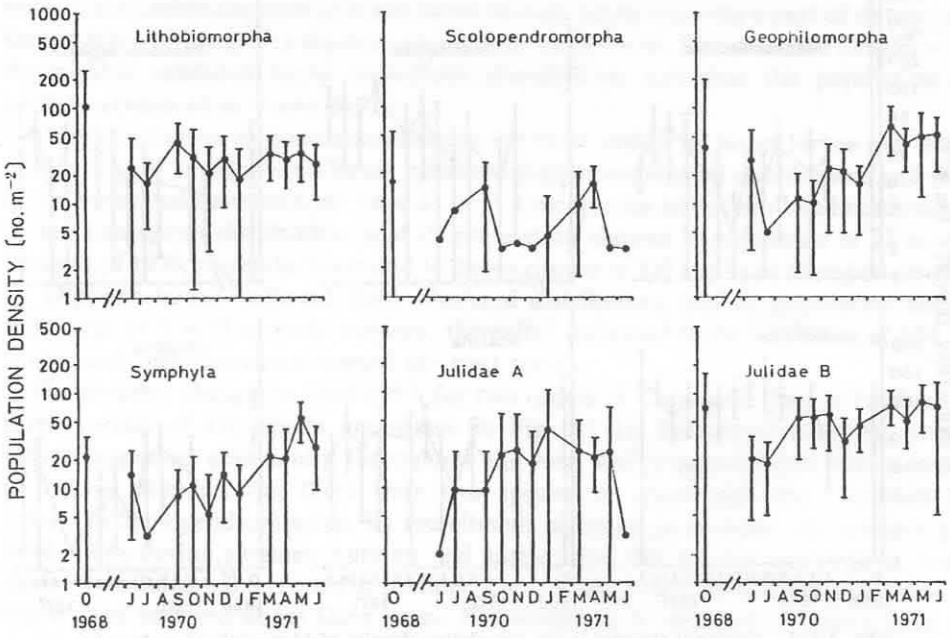

FIG. 3.1–8. Seasonal changes in the population density of Lithobiomorpha, Scolopendromorpha, Geophilomorpha, Symphyla, Julidae A and Julidae B.

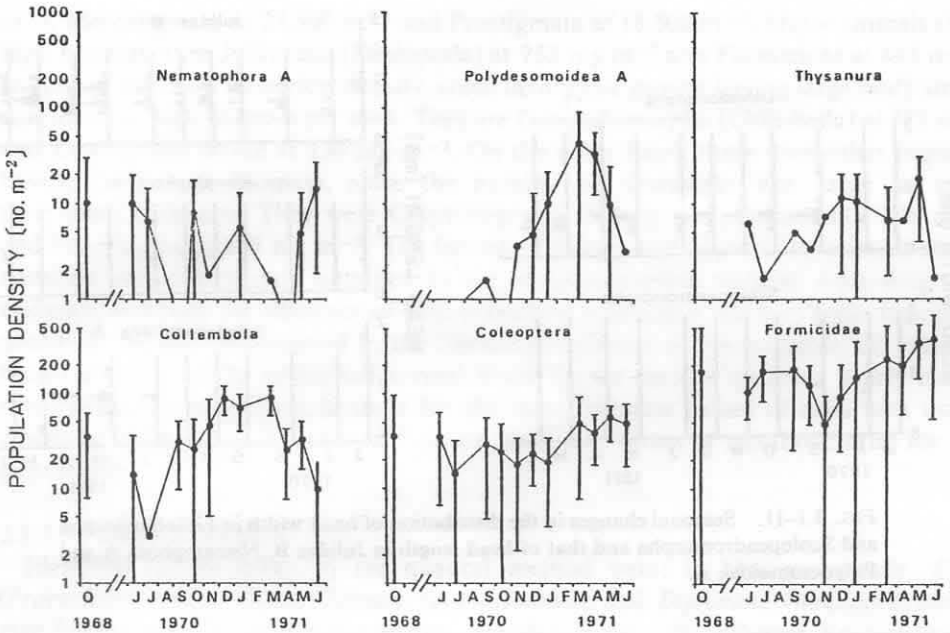

FIG. 3.1–9. Seasonal changes in the population density of Nematophora A, Polydesomoidea A, Thysanura, Collembola, Coleoptera and Formicidae.

random or slightly aggregated distribution, and its population showed its minimum of 18 m^{-2} in July, 1970 and then increased to its maximum of 78 m^{-2} in May, 1971.

The monthly changes in population density for two species of Diplopoda, Thysanura, Collembola, Coleoptera, and Formicidae are presented in Fig. 3.1–9. The population of Nematophora A was its maximum of 14 m^{-2} in June, 1971, and none of them were found in September, 1970 or in April, 1971. Polydesomoidea A exhibited fairly contagious distribution, and its population was small in number in summer, increased to its peak in the next spring, and then decreased. The number of animals was at a maximum of 43 m^{-2} in March, 1971. Thysanura showed a considerable clumping trend in their distri-

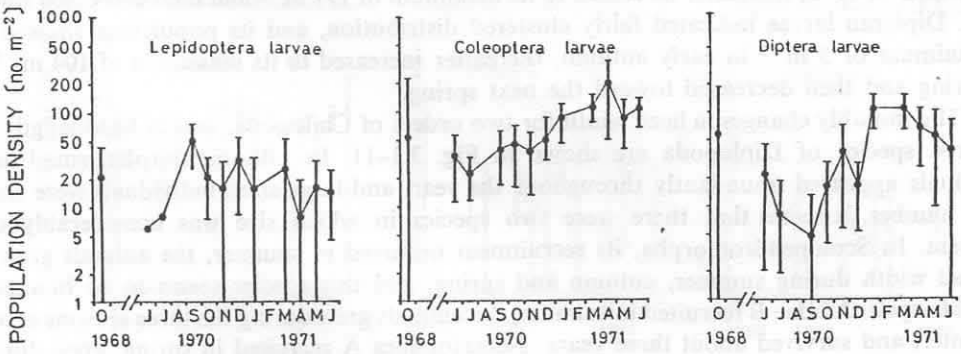

FIG. 3.1–10. Seasonal changes in the population density of Lepidoptera, Coleoptera and Diptera larvae.

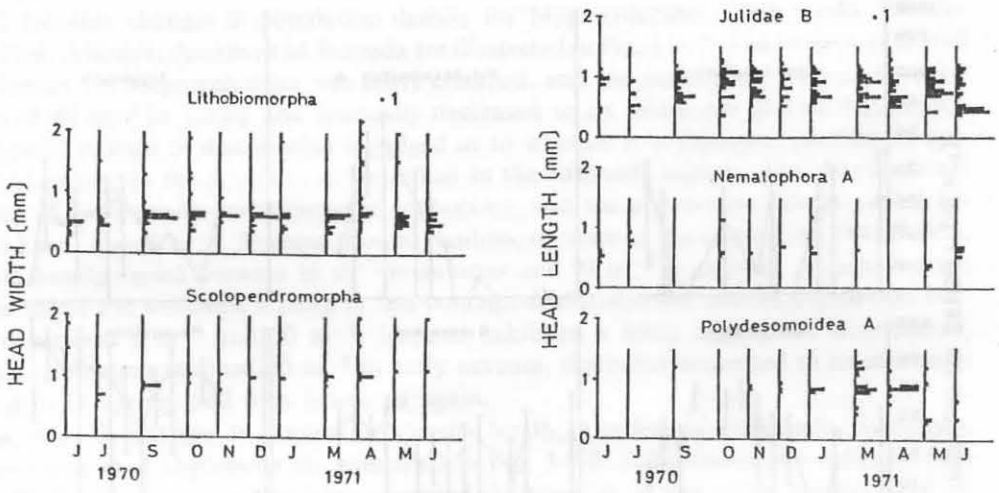

FIG. 3.1–11. Seasonal changes in the distribution of head width in Lithobiomorpha and Scolopendromorpha and that of head length in Julidae B, Nematophora A and Polydesomoidae A.

bution, and the population was at a minimum of 2 m^{-2} in summer, thereafter increased to its maximum (18 m^{-2}) in spring and then decreased. Collembola collected by hand showed random or more or less aggregated distribution, and its population was at a minimum of 3 m^{-2} in summer, thereafter increased to 92 m^{-2} in winter and then declined. Coleoptera indicated a fairly clustered distribution, and its population fluctuated between 14 and 58 m^{-2}. The formicid population in soil down to 7 cm depth was only a part of its total population in layer of nearly 1 m depth to which their nests reach. However, the data showed that Formicidae exhibited fairly contagious distribution, and that the population density varied between 46 m^{-2} and 337 m^{-2}.

Monthly changes in population density for three orders of insect larvae are illustrated in Fig. 3.1–10. Lepidopteran larvae indicated slightly aggregated distribution, and its population fluctuated between 6 m^{-2} and 51 m^{-2}. Coleopteran larvae exhibited random or more or less contagious distribution, and its population showed its minimum of 22 m^{-2} in the summer of 1970, thereafter increased to its maximum of 197 m^{-2} and then decreased slightly. Dipteran larvae indicated fairly clustered distribution, and its population showed its minimum of 5 m^{-2} in early autumn, thereafter increased to its maximum of 104 m^{-2} in spring and then decreased toward the next spring.

The monthly changes in head width for two orders of Chilopoda, and in head length for three species of Diplopoda are shown in Fig. 3.1–11. In Lithobiomorpha, small individuals appeared abundantly throughout the year, and large-sized individuals were small in number. It seems that there were two species in which size was considerably different. In Scolopendromorpha, its recruitment occurred in summer, the animals grew in head width during summer, autumn and spring, and this species seems to be bi-annual in life cycle. Julidae B recruited in summer, the animals grew during the three seasons except winter, and survived about three years. Nematophora A recruited in spring, grew during spring, summer and autumn, and survived about two years. Polydesomoidea A recruited in late spring, grew during the seasons except winter, and survived about three years.

3.1.2.4 Comparison of Estimates by the Four Methods

The estimates of population density and biomass are shown in Table 3.1–3 for the various taxonomic groups of soil invertebrates in October, 1970. Population density estimated by Tullgren's funnel method was higher than that estimated by the quadrat method for all groups of animals. However, biomass for Araneae and Coleoptera larvae assessed by the quadrat method was higher than that assessed by Tullgren's funnel method. For large-sized Gastropoda, Nematophora, Geophilomorpha, Scolopendromorpha, Lithobiomorpha and Lepidoptera larvae, specimens were taken only by the quadrat method.

Animals having abundant population estimated by the four methods were Nematoda at 6.29×10^6 m^{-2}, Enchytraeidae at 70,900 m^{-2}, Collembola at 59,720 m^{-2}, Cryptostigmata at 37,120 m^{-2}, and Diptera larvae at 34,000 m^{-2}.

Animals showing high biomass were Enchytraeidae at 2687 mg (dry weight) m^{-2}, Juliformia at 1498 mg m^{-2}, Formicidae at 813 mg m^{-2}, Nematoda at 604 mg m^{-2}, Megascolecidae at 505 mg m^{-2}, and Diptera larvae at 408 mg m^{-2}.

TABLE 3.1–3. Population density and biomass estimated by methods of Baermann's funnel, O'Connor's funnel, Tullgren's funnel and quadrat in October, 1970.

Methods	Population density (no m^{-2})				Biomass (dry wt mg m^{-2})			
	Baermann's funnel	O'Connor's funnel	Tullgren's funnel	Quadrat	Baermann's funnel	O'Connor's funnel	Tullgren's funnel	Quadrat
Nematoda	6,290,000				604			
Gastropoda				19.2				194
Enchytraeidae		70900				2687		
Megascolecidae			830	11.2				505
Pseudoscorpione			60				10	
Mesostigmata			17660				60	
Prostigmata			13060	6.4			6	
Astigmata			4610				2	
Cryptostigmata			37120				79	
Araneae			130	94.4			12	118
Isopoda			60	14.4			9	6
Nematophora				8.0				11
Juliformia			190	78.4			1498	773
Geophilomorpha			33	9.6			189	34
Scolopendromorpha				3.2				5
Lithobiomorpha			175	30.4			60	22
Symphyla			380	11.2			6	—
Protura			60				—	—
Collembola			59720	25.6			86	—
Diplura			60				—	
Thysanura				3.2				—
Thysanoptera			60				—	
Coleoptera			260	24.0			29	6
Formicidae			7680	120.0			813	13
Hemiptera larvae			60				—	
Lepidoptera larvae				20.8				75
Diptera larvae		34000	320	16.0		408	5	—
Coleoptera larvae			60	44.8			13	152

3.1.3 Oxygen consumption by populations

Oxygen consumption by an animal population is one of the important indices which indicate ecological activity. A lot of information on bio-economics has been accumulated through intensive studies made by many authors on oxygen consumption by animal populations and the energy flow through them.

In this section, energy flow through soil invertebrate populations in terms of respiration is estimated using this information and data on their biomass. The following coefficients are necessary for estimating oxygen consumption: C, the caloric contents of body tissues, R/B, denoting the respiration/mean biomass ratio, F, the efficiency coefficient of extractors, and Q representing the correcting factor for temperatures different from the Minamata area. Coefficient C, for each group of animals, is cited from the references. Coefficient R/B is not always described in papers dealing with bio-economics. In such a case, it is necessary to calculate the R/B using estimated results in the paper and adequate conversion factors. When there are several values of R/B for each group of animals, an averaged value is utilized. When there is no value of R/B for any group of animals, a value for an animal which resembles the group in life form and in body size is adopted as the R/B. Coefficient F is not known for Enchytraeidae or insect larvae. It is unusual to assume that the extractor efficiencies for such animals are high. But we adopted an efficiency of 100% for such animals because there were no data.

Now let us consider the coefficient Q. Intensive bio-economic studies have been made in Europe and America. The yearly mean temperature in the Minamata area may be higher by about 10° C than that in Europe or in the colder regions of America. We compared the R/B values for taxonomically close groups of animals. For populations belonging to *Onychiurus* (Collembola), the R/B of *O. procampatus* studied by Healey (1967) in England was 5.6. On the other hand, that of *O.* (*Protaphorura*) sp. studied by Tanaka (1970) in Japan was 13.2. For the R/B of *Ligidium hypnorum* (Isopoda) studied by Stachurski (1974) in Poland the value was 6.2. On the other hand, that of *L. japonicum* studied by Saito (1969) was 14. It is found from these facts that the conversion factor, Q of 2 must be considered, when the R/B for animals in Europe or in colder regions of America is used as a substitute for animals in the Minamata area.

Table 3.1–4 shows mean population density, mean biomass, coefficients C, R/B, F, and Q, and oxygen consumption for each taxonomic group of soil invertebrates. Animals having high population densities were Nematoda (3.23×10^6 m^{-2}), Collembola (66,000 m^{-2}), Cryptostigmata (65,800 m^{-2}), Enchytraeidae (56,040 m^{-2}), and Dipteran larvae (34,000 m^{-2}). Animals showing high biomasses were Enchytraeidae (2687 mg m^{-2}), Juliformia (773 mg m^{-2}), Formicidae (445 mg m^{-2}), and Diptera larvae (408 mg m^{-2}). If the efficiency of extractors is taken into consideration, the following estimates can be made for the population density of the major animals: Nematoda (4.85×10^7 m^{-2}), Collembola (2.64×10^5 m^{-2}), Cryptostigmata (1.65×10^5 m^{-2}), and Mesostigmata (6.88×10^4 m^{-2}).

Animals consuming high energy through respiration are Nematoda (1326 kcal m^{-2} y^{-1}), Enchytraeidae (511 kcal m^{-2}y^{-1}), Formicidae (136 kcal m^{-2}y^{-1}), Diptera larvae (77 kcal m^{-2}y^{-1}) and Collembola (67 kcal m^{-2}y^{-1}). Total respiration rate for the animals described above attains 2117 kcal m^{-2}y^{-1}, and this value constitutes 93% of total respiration (2277 kcal m^{-2}y^{-1}) for all soil invertebrates (cf. Table 3.1–5). Nishioka et al. (1978), estimated litter fall at 647 g m^{-2}y^{-1} in plot P2 near this sampling area. The caloric equivalent for this litter size may be assessed as 2912 kcal m^{-2}y^{-1} using 4.5 kcal g^{-1} (dry weight) (Cummins and Wuycheck, 1971) for calorific contents of the litter. Energy flow

TABLE 3.1–4. Population density, biomass, caloric contents, respiration/mean biomass ratio, efficiency of extractor, correction factor for activity, and oxygen comsumption for population of soil invertebrates. See text for details.

	Population*1 density (no m^{-2})	Biomass*6 (mg m^{-2})	Caloric*8 contents (cal mg^{-1})	Respiration/ mean biomass	Efficiency coef. of extractors	Correction for activity	Respiration (kcal $m^{-2}y^{-1}$)
Nematoda	3,230,000*2	239*2	5.7	32.5*14	15*23	2	1326
Gastropoda	130	194*4	1.4*9	2.5*15	1	2	1
Enchytraeidae	56,040*3	2687*5	5.4	17.6*16	1	2	511
Megascolecidae	495	505*7	5.05*10	10.7*10	1	1	27
Pseudoscorpione	335	16	4.8	16.6*17	5*24	1	6
Mesostigmata	27,500	103	4.8	16.6*17	2.5*24	1	21
Prostigmata	18,500	12	4.8	16.6*17	2.5*24	1	2
Astigmata	6,050	2	4.8	4.5*18	2.5*24	2	—
Cryptostigmata	65,800	160	4.8	4.5*18	2.5*24	2	17
Araneae	240	118*7	4.8	16.6*17	1	1	9
Isopoda	78	18	3.8*11	11*19	1	1	1
Nematophora	15*4	11*7	3.5*12	1.3*20	1	1	—
Juliformia	685	773*7	3.5*12	1.3*20	1	1	4
Geophilomorpha	33	189	4.8	16.6*17	1	1	15
Scolopendromorpha	7*4	5*7	4.8	16.6*17	1	1	—
Lithobiomorpha	175	60	4.8	16.6*17	1	1	5
Symphyla	560	14	4.8	22.2*21	4*21	1	6
Protura	350	—					—
Collembola	66,000	126	6.0*13	22.2*21	4*21	1	67
Diplura	4*4	—					—
Thysanura	3*4	—					—
Thysanoptera	175	—					—
Coleoptera	353	68	5.6	8.5*22	3*24	2	19
Formicidae	2,930	445	4.5	8.5*22	4*24	2	136
Hemiptera larvae	703	31	5.5	8.5*22	1	2	3
Lepidoptera larvae	290	130	5.5	8.5*22	1	2	12
Diptera larvae	34,000*5	408*5	5.4	17.6*16	1	2	77
Coleoptera larvae	223	125*7	5.5	8.5*22	1	2	12

*1, four months mean figure estimated by Tullgren's funnel method; *2, five months mean figure through Baermann's funnel; *3, five months mean figure through O'Connor's funnel; *4, eleven months mean figure estimated by quadrat method; *5, figure through O'Conner's funnel in October, 1970; *6, four months mean figure through Tullgren's funnel; *7, value estimated by quadrat method in October, 1970; *8, Cummins & Wuycheck, 1971; *9, quoted from Cummins & Wuycheck, 1971, and Mishima, 1971; *10, Sugi, 1978b; *11, quoted from Cummins & Wuycheck, 1971, and Saito, 1967; *12, Saito, 1967; *13, Healey, 1967; *14, Wasilewska, 1974, *15; Richardson, 1975; *16, O'Connor, 1963; *17, van Hook, 1971 and Moulder et al., 1972; *18, Webb, 1970; *19, Saito, 1969; *20, Saito, 1967; *21, Tanaka, 1970; *22, Wiegert, 1965; *23, Sugi, 1971; *24, Niijima et al., 1968.

TABLE 3.1–5. Oxygen consumption (kcal $m^{-2}y^{-1}$) by major groups of soil animals. Figures in parentheses show population density ($\times 10^4$ m^{-2}).

	Managed grass field Nielsen (1961)	Unutilized pasture Wasilewska (1974)	Blanket bog Standen (1973)	Coniferous forest O'Connor (1963)	Spruce raw humus Macfadyen (1963)	Spruce stand Huhta et al. (1975)	Subalpine coniferous forest Kitazawa et al. (1977)	Subtropical rain forest Kitazawa (1971)	Evergreen oak forest (Present authors)
Nematoda	343* (10^3)	65 (370)			92	4 (141)	26 (207)	13 (23)	1326 (323)
Enchytraeidae	155* (7.4)		63 (4.3)	151* (13.4)	1	10 (1.3)	92 (13.6)	42 (1.0)	511 (5.6)
Lumbricidae					1	16	1.3		
Megascolecidae								19	27
Collembola					61	3 (4.6)	14 (3.7)	346 (6.4)	67 (6.6)
Oribatei					21	6 (21.2)	8 (1.4)	23 (8.5)	17 (6.6)
Other Acari					134	4 (11.0)	(2.1)		23 (5.2)
Chilopoda					9	1	0.8	8	20
Araneae					—	1		4	9
Formicidae									136 (0.2)
Coleopterous adult					34	1		1	19
Coleopterous larvae					—	2		1	12
Dipterous larvae					27	3		17 (0.1)	77 (3.4)

Note: asterisks show that figures were calculated by use of 4.83 cal/ml O_2.

consumed by respiration through soil invertebrates attained 78% of the total litter fall per year.

3.1.4 *Discussion*

A bio-economic study on soil invertebrates in an evergreen oak forest was made by Kitazawa (1971), who called it by the name of subtropical rain forest as shown in Table 3.1–5. The results derived from Kitazawa (1971) will be compared with those of the present study. The ratio of population density of the former to that of the latter is 1/10 for Nematoda, 1/5 for Enchytraeidae, 1 for Collembola and Acarina, and 1/30 for Dipteran larvae. Oxygen consumption by Nematoda in the present study is about one hundred times larger than that of Kitazawa's study. This large value in the present study is based on an extractor efficiency of 1/15, and the population density of Nematoda in the present study area is about ten times as large as that in Kitazawa's study area. Enchytraeidae in the present study consumed more than ten times as much oxygen as in Kitazawa's study. On the other hand, oxygen consumption of Collembola is one-fifth as much as in Kitazawa's study area. This value seems to be too high for us to believe. This doubt is derived from the fact that in spite of there being no difference in environmental conditions in the two study areas, and in spite of almost the same number of Collembola in both areas, the activity of Collembola in Kitazawa's study area is more than three times as high as that of *Isotoma* (*Desoria*) *trispinata*, the most active species of Collembola (Tanaka, 1970). In Kitazawa's study, the activity of Collembola was by far the highest of all animals, although we cannot decide whether the activity of Collembola was overestimated, or that of other animals was underestimated. Oxygen consumption of Diptera larvae in the present study is about five times as much as that in Kitazawa's study. Formicidae in the present study area show a considerably high metabolic rate, but this value cannot be compared with Kitazawa's, because he did not estimate the metabolic rate of Formicidae. If the population of Formicidae inhabiting soil deeper than the depth used in the present study is considered, the population density of Formicidae will become several times larger, and then the metabolic rate will become several times that in the present study. This value is fairly high in comparison with the values for other animals.

Some features of the population density of soil invertebrates in temperate regions of Europe and Japan, and in the warm temperate region of Japan can be derived from Table 3.1–5. The population density of Nematoda is about 10^7 m^{-2} order in the soils of both regions. That for Enchytraeidae is about 10^5 m^{-2} in forest soils of the temperate region, and is about $5 \times 10^4 m^{-2}$ in the pasture soils of the temperate region and in forest soils of the warm temperate region. The major group of earthworms in the temperate region is Lumbricidae. On the other hand, that in the warm temperate region is Megascolecidae. The population density for Collembola in both regions is about 5×10^4 m^{-2}. That for Oribatei fluctuates between 10^4 m^{-2} and 10^5 m^{-2}. There are a lot of Formicidae in the soils of the warm temperate region.

Soil animals having high respiration rates along with values from previous studies are shown in Table 3.1–5. We can see that Nematoda and Enchytraeidae usually show high respiratory rates in temperate and warm temperate regions. Oxygen consumption values obtained in the present study are by far the highest of all. This result is due to consideration of extractor efficiency. If other authors estimate oxygen consumption considering the efficiency of extractors, the corrected value will become many times the uncorrected value. Oxygen consumption by soil animals during a year attained several tens per

cent. of the caloric content of total litter fall. As described in the previous section, the present study showed that the total animal oxygen consmuption constituted 78% of litter fall.

The extraction efficiency of Tullgren's funnel has been studied by several authors (Forsslund, 1948; Macfadyen, 1953 and Niijima et al., 1968) for some groups of animals, and also has been studied by Tanaka (1970) (efficiency, which depends on the size of animals, is about 25% on the average), and by Tamura (1976a) (22%) for each size of the dominant species of Collembola. The efficiency of Baermann's funnel extractor for Nematoda has been studied by Sugi (1971) (efficiency depends on the species, and ranges from 1 to 17%), and by Harasawa (in Kitazawa et al., 1977) (about 30%). These studies have shown that the efficiency of extractors is not good for all groups of animals, and these authors have mentioned that it is necessary to take into consideration the efficiency of extractors in estimating population density, biomass and so on. However, there have been few studies of natural populations based on extractor efficiency except for those on *Isotoma* (*Desoria*) *trispinata* and *Onychiurus* (*Protaphorura*) sp. (Collembola) made by Tanaka (1970), on *Folsomia octoculata* (Collembola) made by Tamura (1976b), and on Nematoda made by Kitazawa et al. (1977). Huhta and Koskenniemi (1975) estimated the oxygen consumption of soil invertebrates by the use of extractor efficiency, but they did not consider the absolute efficiency, which means the ratio of the number of animals extracted with an extractor to that found in the soil.

In the future, it will be necessary to make ecological studies based on the efficiency of the extractors, since the absolute population density of soil animals is several times as high as the estimate of density of extracted animals as mentioned above. This knowledge enables us to predict that the efficiency of an extractor depends on the animals or species. It may well be that, in comparing the sampling sites for species composition of soil animals, the wrong conclusions will be derived if the efficiency of extractors is not considered.

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